

A description of additional variation seen in the scale morphology of the Frasnian thelodont *Australolepis seddoni* Turner and Dring, 1981

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Abstract – Isolated scales are referred to the thelodont *Australolepis seddoni* from the (Frasnian) Gneudna Formation, Carnarvon Basin, Western Australia. A total of 670 scales was examined in comparison to the original sample of 60 scales, and it is considered that the majority of these scales represent morphological variation within *A. seddoni*. The scales were then assigned to different body regions based on their morphology. In addition to *A. seddoni* scales, two other scale types were recognized and these were referred to the genus "*Skamolepis*." The presence of this genus in the Gneudna Formation suggests a close link between the faunas of Western Australia and central Iran.

INTRODUCTION

The first thelodont scales to be described from Frasnian aged sediments occur in the Gneudna Formation, Carnarvon Basin, Western Australia (Turner and Dring 1981). This occurrence extended the range of thelodonts to the Upper Devonian. However, to date Frasnian thelodonts are only recorded from Gondwanan strata (Turner 1997). The original description of *Australolepis seddoni* Turner and Dring, 1981, was based on a scale sample of about 60 specimens from the middle of the type section (KT beds 13–15), which were referred to head, trunk and transitional scales based on the system of Gross (1967) which was then in use. These scales were distinctive in having highly crenulated crowns, and navicular or horn-like ridges, often bifurcated at the perimeter of the crown.

Further sampling of the Gneudna Formation has yielded many more thelodont scales, allowing a greater understanding of the intraspecific variation within *A. seddoni*, and resulting in another six scale types (*sensu* Märss 1986) being described. Four of the additional scale variants are transitional scales and show a gradation into the "nikoliviid" scale type. Turner and Dring (1981) originally considered this tripartite crowned scale as a separate species, *nikoliviid* gen. *et* sp. *indet.* However, Turner (1993, 1997) considered these scales as variants of *A. seddoni*. After taking into consideration the increased variation in scale morphology within *A. seddoni*, scales previously referred to as *Turinia* sp. cf. *antarctica* from the Gneudna Formation, Western Australia (Long and Trinajstić in press) are now referred to *A. seddoni*. One other thelodont scale type, with a flattened and posteriorly flaring crown,

has been found in the Gneudna Formation and this is described and referred to the genus "*Skamolepis*" Turner and Janvier, 1979.

Through the study of articulated specimens, considerable variation in the morphology of scales has been observed in many thelodont species (Gross 1967, 1968; Karatajute-Talimaa 1978; Märss 1986; Turner 1976). With reference to the new scale variants of *A. seddoni* described, the possible range of morphological variation within *A. seddoni* is discussed. Based on the morphological variation studied in several articulated thelodont genera, Märss (1986) described a pattern of squamation based on five distinct morphological areas, providing a uniform reference for the identification of isolated thelodont scales. The possible body regions from which the scales of *A. seddoni* originated are discussed in reference to the five regions defined by Märss (1986).

MATERIALS AND METHODS

The thelodont scales described are from the type section of the Gneudna Formation, Williambury Station, Western Australia (Figure 1). Scales described in this paper come from the residue of limestone samples digested in 10% acetic (Rixon 1979). A total of 670 scales was examined in comparison to the original sample of 60 scales. The scanning electron micrographs were made on a Philips 505 at the Centre for Microscopy and Microanalysis, The University of Western Australia. Thin sections of scales were made by handgrinding and examined under confocal and light microscopes. Specimens have been deposited in the collections of the Western Australian Museum (WAM).

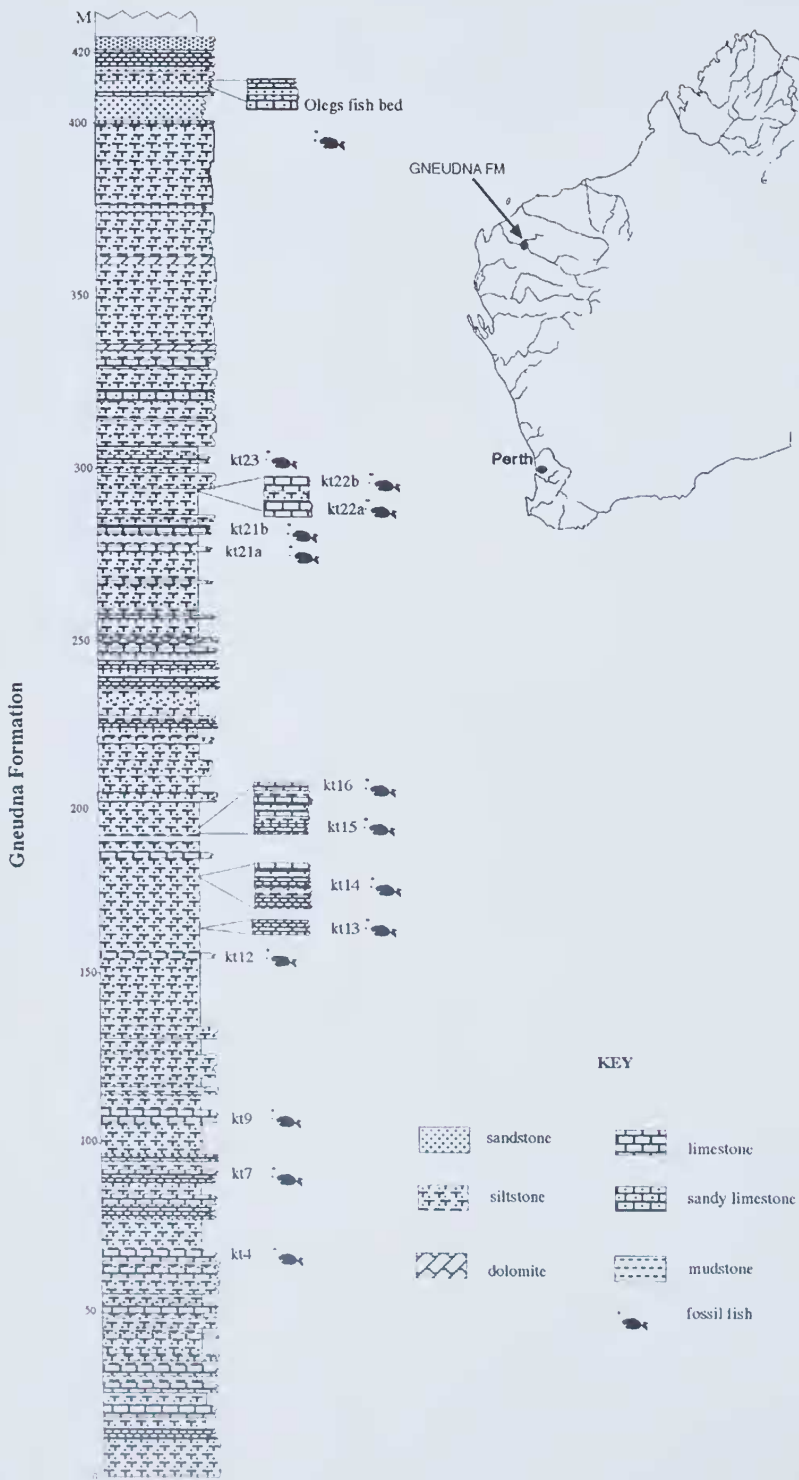


Figure 1 Stratigraphic column indicating the beds in which thelodonts occur in the Gneudna Formation and a map of Western Australia showing the location of the Gneudna Formation

SYSTEMATIC PALAEOLOGY

Superclass Agnatha

Class Pteraspidomorphi

Subclass Thelodonti

Order Thelodontida

Family Turiniidae Obruchev, 1964

Genus *Australolepis* Turner and Dring, 1981*Australolepis seddoni* Turner and Dring, 1981

Emended Diagnosis

A scale species with major crown ribs that often have an ornament of small tubercles. Scales are small to medium-sized, mostly 0.5–1mm long. Those scales with lappets also have a pronounced, fine ribbed micro-ornament. Trunk scales are often characterised by multidigitate lappets. Scales show a typical turiniid histology.

Remarks

The scales described in this study represent variants of *A. seddoni* not formally described. They differ from previously described *A. seddoni* scales (Turner and Dring, 1981) in possessing a micro-ornament of fine parallel ribs, tubercles on the main ribs and upward projecting neck spurs. *A. seddoni* scales can be separated from the scales of *Turinia antarctica* Turner and Young, 1992 by the absence of minor rib tubercles, the absence of narrow troughs subdividing major crown ribs, and the generally greater complexity of the crown ribbing. *A. seddoni* scales can be separated from the scales of *Turinia pagoda* Wang *et al.*, 1986 by the more delicate and deeply dissected crowns, and the less developed neck spurs found in *A. seddoni*. The absence of double ribs in *A. seddoni* scales separate them from scales of *Turinia gavinyoungi* Turner, 1995 and *Turinia hutkensis*.

Description of scale variants in *A. seddoni*

Scale Type 1

Material

20 scales WAM 99.8.15–18 (Figure 2A–B)

Horizon

KT beds 4, 12, 13, and 14 (Figure 1).

Description

The scale is sub-rounded in outline. There are eight ribs radiating from a high, rounded central apex to a narrow, shallow neck (Figure 2A). Wide troughs separate the ribs. The ribs all

bifurcate at the interface with the crown neck. At the distal margin of each rib are six rounded tubercles (Figure 2B), similar to those seen in *T. antarctica* (Turner and Young, 1992, figure 4a–e). In addition to the tubercles, is a micro-ornament of fine, parallel ribs, which is present on the distal margin of each rib and along the apex of each rib (Figure 2B). Although *A. seddoni* type 1 scales are similar to *T. antarctica* scales, they are differentiated by the lower number of ribs, the lower number of rib tubercles and the absence of double ribbing. The base is slightly wider than the crown, and there is a low neck. There are no neck-spurs present, but there are twelve bean-like swellings around the basal pulp cavity, similar to the swellings seen in the type sample of *A. seddoni* and *T. pagoda* (Wang *et al.*, 1986, figure 5A–B).

Scale Type 2

Material

10 scales WAM 99.8.19–21 (Figure 2C)

Horizon

KT beds 4, 12, and 14 (Figure 1).

Description

These broad scales are low in profile. The apex of the crown is positioned above the posterior third of the scale (Figure 2C). Two posteriorly bifurcating ribs dissect the anterior scale face. Along the apex of the bifurcated ribs are small tubercles, similar to those present in scale type 1. Two deep troughs separate the lateral lappets projecting from below the crown apex, from the anterior portion of the crown. Posteriorly, the apex terminates in three deep ribs. The posterior lateral lappets have a micro-ornament of fine, parallel ribs (Figure 2C). These scales appear similar to a transitional scale figured by Turner and Dring (1981, figure 4J). They can be distinguished from this scale type by the presence of tubercles on the anterior ribs, and by the micro-ornament present on the posterior lappets (Figure 2C).

The flat base is wider than the crown, and there is a wide pulp cavity. In this respect the base does not differ from previously described *A. seddoni* scales (Turner and Dring 1981).

Scale Type 3

Material

20 scales WAM 99.8.22–25 (Figure 2D)

Horizon

KT beds 4, 12, 13 and 14 (Figure 1).

Description

The crown of scale type 3 is tripartite (Figure 2D). The anterior face of the crown has two prominent ribs which bifurcate close to the interface of the crown with the neck. The central section of the crown is triangular and there is a wide plateau extending to form two lateral lappets. The lappets branch at the distal margins. The third division of the crown consists of a single, median rib with two bulbous projections off each side. The elliptical base is wider than the crown, and does not possess an anterior spur. There is a large pulp cavity in the base of the scale.

Scale Type 4*Material*

18 scales WAM 99.8.26–30 (Figure 2E)

Horizon

KT beds 4, 12, 13, 14 and 15 (Figure 1).

Description

These scales are high crowned with acute apices (Figure 2E). The anterior face has one prominent rib that branches approximately halfway along to form three ribs. On the posterior margin of the crown are two elongate spurs, projecting upwards. The location and shape of the neck spurs are similar to those on the body scales of *T. pagoda* (Wang *et al.*, 1986, figure 4a–f). However, there are far fewer neck spurs on *A. seddonii* scales. There is a shallow, narrow neck. The base of the scale is narrower than the crown and there is no anterior process. There are six bean-like projections around the basal pulp canal similar to those found in *T. pagoda* (Wang *et al.*, 1986).

Scale Type 5*Material*

20 scales WAM 99.8.31–34 (Figure 2F)

Horizon

KT beds 4, 12, 13 and 14 (Figure 1).

Description

This medium sized, navicular scale has four ridges on the anterior face of the crown which converge, and taper posteriorly towards a high apex (Figure 2F). There is an ornament of small tubercles along the distal third of the ribs, near the crown-neck interface. The posterior region of the scale is divided into three sections by narrow ridges which terminate in three small, upturned neck-spurs, similar to those in *T. pagoda* (Wang *et al.*, 1986). The neck is a smooth, narrow furrow, and the base is slightly larger than the crown. There is a small anterior process on the base (Figure 2F). There are

six small, bead like swellings around the basal pulp cavity. This scale type, in the presence of upturned neck-spurs and bead like swellings around the basal pulp cavity, resembles trunk scales of *Turinia pagoda* (Wang *et al.*, 1986, figure 6 A). The scale is distinguished from *T. pagoda* by the high crown apex, lesser development of the neck-spurs and the absence of micro-ornament.

Scale Type 6*Material*

15 scales WAM 99.8.35–37

Horizon

KT beds 4, 12 and 14 (Figure 1).

Description

In scale type 6, the anterior face of the crown has a well-defined, bifurcated rib. This extends from the margin of the scale, and terminates almost at the crown apex. The scale is separated into three sections by highly developed, ridged lateral lappets. Both sets of lappets curve posteriorly. The base is wide, with a small anterior process, and the neck is shallow. The lack of micro-ornament distinguishes this scale from superficially similar *Turinia antarctica* scales (Turner and Young, 1992).

Scale Type 7*Material*

12 scales WAM 99.8.38–41 (Figure 2G)

Horizon

KT beds 4, 12, 13 and 14 (Figure 1).

Description

In this scale type the crown is divided into three sections. The anterior face of the crown has two prominent ribs which bifurcate approximately halfway down each rib. The ribs have a slightly scalloped appearance. The middle section of the crown also has two ribs and these extend outward, with two wide lateral lappets forming off the distal end of each rib. The lappets branch at the lateral margins, with each branch terminating in a rounded tubercle. There is a micro-ornament of parallel ribs on the most distal portion of the lappets. The third division of the crown consists of a single median rib with two narrow lappets projecting off each side. The elliptical base is wider than the crown and does not possess an anterior spur. There is a large pulp cavity in the base of the scale.

Scale Type 8*Material*

17 scales WAM 99.8.42–45 (Figure 2H & I)

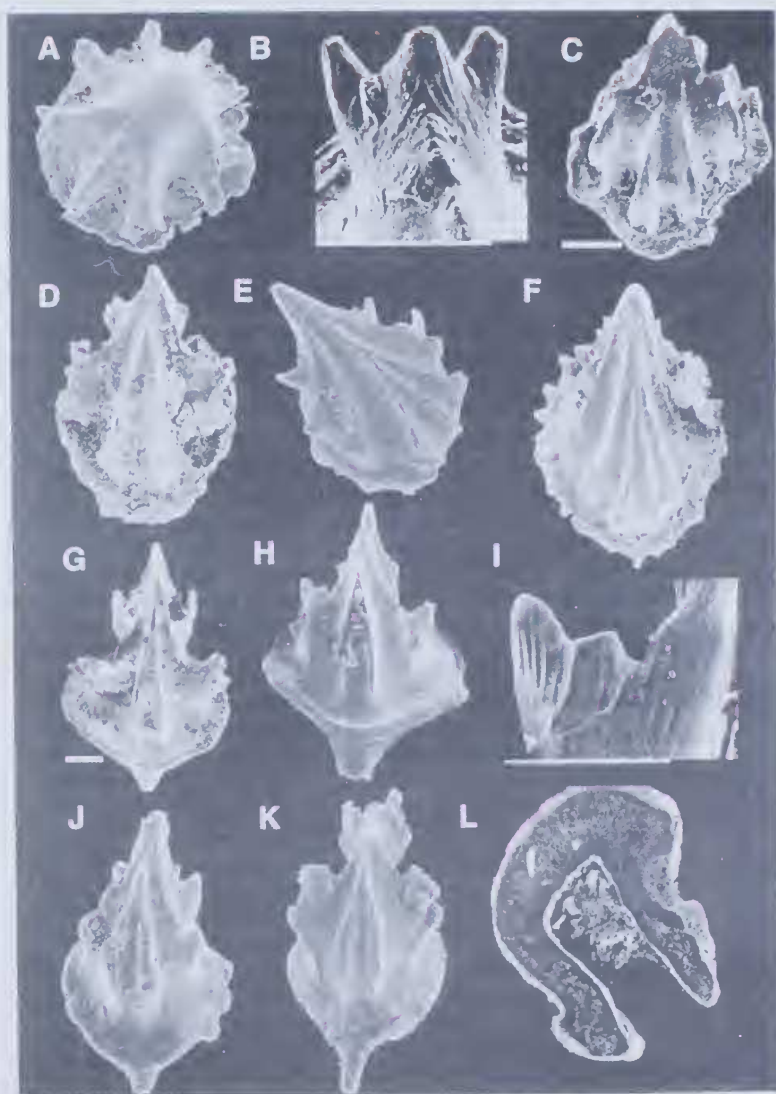


Figure 2 Scales designated as *Australolepis seddoni*. A-B morphotype 1 - oral scales, C morphotype 2 - cephalopectoral scales, D morphotype 3 - post-pectoral scales, E morphotype 4 - pre-caudal scales, F morphotype 5 - pre-caudal scales, G morphotype 7 - pre-caudal scales, H-I morphotype 8 - pre-caudal scales, J morphotype 9 - fin scales, K morphotype 10 - fin scales, L Thin section of morphotype 1 scale photographed under a confocal microscope. Scale Bars A, C- H, J-L = 1.0mm, B, I = 0.1 mm.

Horizon

KT beds 4, 12, 14 and 22 (Figure 1).

Description

The crown of scale type 8 is almost identical to scale type 7. The primary difference occurs in the central section of the crown. Here the ribs continue to the base, the lappets forming behind the main ribs. Each lappet projects posteriorly and is dissected by a single strong rib. The micro-ornament is more developed in this scale

compared to the scales previously described (Figure 2I). Fine parallel ribs are present on the lappets, the anterior edges of the middle section of the crown, and on the posterior section of the crown where they continue half way down the crown face. In this respect these scales are more similar to the scales of *T. antarctica* (Turner and Young 1992). The base differs considerably from the other scales described, being laterally and anteriorly expanded. There is a well developed anterior process on the central anterior margin. A

well developed anterior spur is seen in other Gondwanan thelodonts including *T. pagoda*, *T. antarctica*, *T. hutkensis*, *T. gondwana* Turner, 1989 and *T. australiensis* Gross, 1971.

Scale Type 9

Material

20 scales WAM 99.8.46–49 (Figure 2J)

Horizon

KT beds 4, 12, 13 and 14 (Figure 1).

Description

This scale type has a similar form to the above tripartite scales. However, it is narrower, and the lateral lappets are not as developed. There is a deeply bifurcated single rib on the anterior face. The bifurcation occurs almost at the apex of the rib. The central portion of the scale is formed by two lateral ribs which terminate in one upturned projection. The posterior section of the scale is formed from two ribs again forming from the scale apex. The ribs expand posteriorly and terminate in upturned projections. There is a small amount of micro-ornament on the posterior lappets. The base is wide and anteriorly expanded. There is a small, rounded anterior process. There are several bead like projections towards the posterior margins of the base.

Scale Type 10

Material

20 scales WAM 99.8.50–53 (Figure 2K)

Horizon

KT beds 4, 12, 13 and 14.

Description

This scale is similar to the scale described above having the crown divided into three partitions. On the anterior crown face there are two ribs which are positioned close together and do not bifurcate. The middle section of the crown, like scale type 9, consists of two outwardly projecting ribs which form wide lappets on the distal margin of each rib. These lappets project posteriorly and are crenulated. There is a fine micro-ornament of parallel ribs around the anterior margin of the lappets. The posterior section of the crown consists of a single medium rib which widens posteriorly to form two lateral lappets. The lappets terminate in high acute points with a micro-ornament around the anterior edges. The base of the scale is rounded and is expanded anteriorly. There is a rounded anterior process which is more developed than the anterior process in scale type 9.

Scale Type 11

Material

10 scales WAM 99.8.54–55 (Figure 3A–D)

Horizon

KT beds 13 and 14 (Figure 1).

Description

Scales belonging to scale type 11 have a tripartite crown. There is a single, major rib on the anterior crown face which divides in two, at the midline. There are numerous small rib tubercles along the length of the main rib. The tiered complexity of the crown in scale type 11 is similar to the crown complexity present in *T. gondwana* recorded from Bolivia (Gagnier *et al.*, 1989) and *T. gavinyoungi* (Turner, 1995) recorded from Australia. The crown expands outwards and backwards. There are two sets of well developed lateral, multidigitated lappets that extend well over the base. There is a micro-ornament of fine parallel ribs on the lappets, and on the main body of the scale (Figure 3D). The base is wider than the crown and there is a long anterior process.

Histology (Figure 2L)

All these scales exhibit typical thelodontid histology (*sensu* Gross, 1967) as described in the type specimens described by Turner and Dring (1981). There is a crown of orthodontine and a base of aspidin-like tissue. In thin section fine dentine tubules can be identified radiating from the pulp canal.

Remarks

The increased sample size has yielded eleven new variations of *Australolepis seddoni* scale types. The new morphological features present in these additional scales indicate a closer relationship between *A. seddoni* and the other Gondwanan thelodonts, *T. antarctica*, *T. gavinyoungi*, *T. hutkensis* and *T. pagoda*. The scales of *A. seddoni* with highly developed lappets are very similar in form to *T. antarctica*, *T. gavinyoungi*, *T. gondwana* and *T. hutkensis*. These scales share tripartite subdivision of the crown and multidigitated lappets. There is also considerable similarity noted between *A. seddoni* and *T. gondwana*, as these species also share a tripartite crown, bifurcated ribbing and a large elongated pulp canal opening.

The presence of neck-spurs in two of the new scale type variations increases the number of characters shared between *A. seddoni* and *T. pagoda*. Wang *et al.* (1986) stated a major difference between *T. pagoda* and *A. seddoni* was the absence of neck-spurs however, they did note the resemblance in the basal structure and general crown form of the scales. It is possible to unite *T. pagoda* and *A. seddoni* in the genus

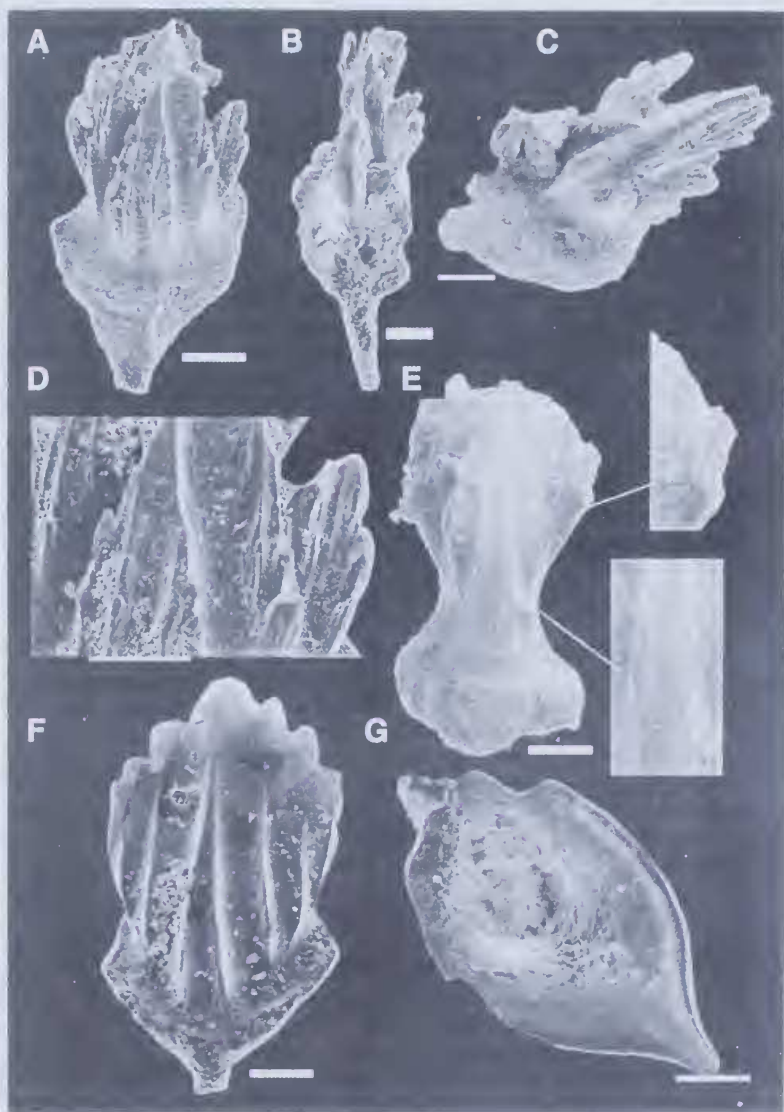


Figure 3 A–D Morphotype 11 scales – fin scales, E morphotype 12 – “*Skamolepis*” scale, F morphotype 13 – “*Skamolepis*” scale, anterior body scales, G morphotype 13 “*Skamolepis*” scale pulp cavity.

Australolepis on the basis of the shared characters: lateral lappets and bead like projections on the base and neck-spurs. However, as the description of *T. pagoda* is based on only six scales it would seem premature to unite these taxa until the full range of variation of *T. pagoda* is known. It is conceivable that all these species represent members of a single Gondwanan genus *Australolepis* (S. Turner and T. Märss, personal communication 1996). A revision of the genus may be required as the Middle and Upper Devonian turiniids of Australia share more in common with those in Antarctica, West Yunnan,

Iran, and Bolivia than with turiniids from the Northern Hemisphere (Turner, 1997).

Allocation of Scale Varieties from *A. seddoni* to Body Regions.

Märss (1986) established that the scale varieties on the articulated specimens of *Phlebolepis* could be distinguished on other thelodonts. Five separate regions with distinct scale morphologies were recognised to occur on individual thelodonts. These were the oral, cephalo-pectoral, postpectoral, precaudal and pinnal regions (Märss, 1986, figure

7). On *Phlebolepis elegans* Pander, 1856, 28 different scale types were determined and on *P. ornata* Märss, 1986 22 different scale types were recognized. With the additional scales described here for *A. seddoni* a total of 28 scale types are now recognised, so it is probable that all these variants did in fact come from the one species.

Scales of type 1 (Figure 2A–B, Figure 4) are considered to represent oral scales (equivalent to head scales of Gross (1967) and Turner and Dring (1981)). Märss (1986) characterises oral scales as having rhombic to rounded crowns with marginal notches and ridges that are orientated toward the crown centre. Cephalo-pectoral scales (transitional scales; Gross (1967) and Turner and Dring (1981)) are large, oval to rhombic scales with short ribs and are generally unsculptured (Märss, 1986). Scales attributed as type 2 (Figure 2C, Figure 4) correspond to this variety. The scales Turner and Dring (1981, figure 6a–c) attributed to nickoliviid type are also considered to represent cephalo-pectoral scales (Figure 4). Post-pectoral scales are represented by scale type 3 (Figure 2D, Figure 4). These scales also lack ornament. The majority of the new scale types described (scale types 4–8) are represented by precaudal scales (Figure 2 E–I, Figure 4). Precaudal scales are characterised by having a wedge shape, a sculptured pattern and a reduced number of lateral ridges (Märss 1986). These scales also commonly have an anterior spur. Scale types 9–10 (Figures 2J–K, 3A–C, 4) represent fin scales. These scales are smaller than the other scale types with a posterior pointed apex, a thin wedged shape and highly sculptured pattern. The suggested body regions from which scales of *A. seddoni* came are shown in Figure 4.

Thelodontida gen. et sp. indet.

Two scale types have been found in the lower section of the Gneudna Formation which resemble scales referred to as "*Skamolepis*" – like by Turner and Janvier (1979) and now referred to *Turinia* sp..

Scale Type 12

Material

5 scales WAM 99.8.56–57 (Figure 3E)

Horizon

KT beds 4 & 12 (Figure 1).

Description

These scales have an unusual shape when compared to other thelodont scales. The crown is slender and flares posteriorly beyond the base. There is an ornamented of parallel single ribs with small tubercles on the rib surfaces. On the lateral margins of the crown are two dorsal side lappets,

each with a fine micro-ornament of narrow ribs. There is a constricted neck on a low round base. The base is as wide as the crown. There is an anterior process. There is a large pulp cavity that widens anteriorly.

Scale Type 13

Material

15 scales WAM 99.8.58–60 (Figure 3F–G)

Horizon

KT beds 4, 12 and 14 (Figure 1).

Description

These scales are similar to scale type 1. It differs in the base being wider and the posterior crown being not as flared, instead terminating in seven rounded projections. The crown is long, projecting over the base posteriorly. It has an ornament of four lateral parallel ribs and a central rib that bifurcates at approximately half the crown height. The neck is very low and there is a central anterior process. On the ventral surface there is a large pulp opening.

Remarks

Scales originally referred to *Skamolepis fragilis* Karatajute-Talimaa, 1978 from the late Emsian to early Eifelian of Europe are now considered to be shark denticles by Turner (1991, 1993). Karatajute-Talimaa (1978) still thinks that the genus *Skamolepis* belong to thelodont scales. Shark denticles which resemble the Baltic scales are still under review. Turner (personal communication 1998) suggests that a new genus may be required for those. However, more material is needed before this can occur.

The scales from the Gneudna Formation closely resemble scales B and C referred to as "*Skamolepis*" (Turner and Janvier, 1979, figure 1, B1–3, C1–3) from the Khush-Yeilagh Formation in Iran (Turner and Janvier, 1979). Scale type 12 also shows some resemblance to a scale referred to *Thelodus trilobatus* from Irian Jaya (Turner *et al.*, 1995). The Gneudna scale however, is higher in profile, the central ridge narrows dorsally (the opposite condition is seen in *T. trilobatus*), and the base extends beyond the lateral and anterior margins of the crown.

DISCUSSION

The range and distribution of thelodonts in Australia has been clarified over the last ten years (Turner 1995, 1997; Young 1995). Since the discovery of Frasnian thelodonts in the Carnarvon Basin, *A. seddoni* has been recorded in Australia from the Virgin Hills Formation, east of Fitzroy Crossing in the Canning Basin and from the Givetian Papilio Formation, Broken River in North Queensland (Turner, 1997). Later, as yet

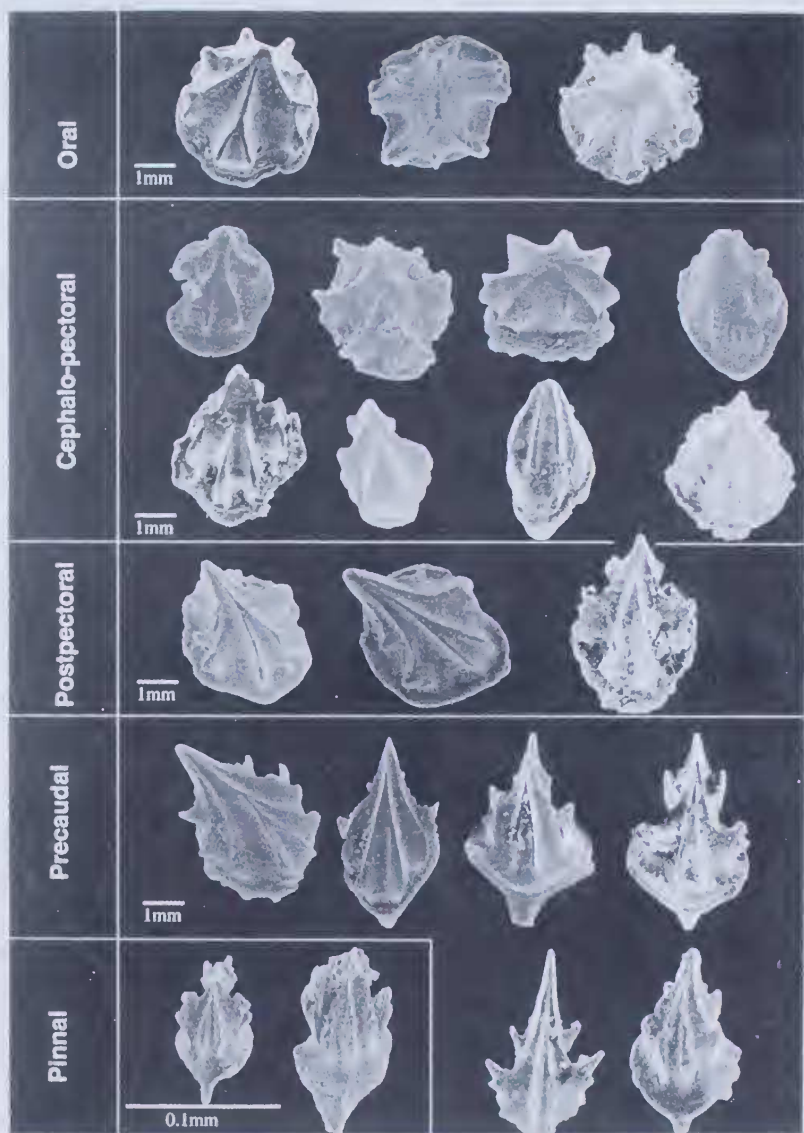


Figure 4 The scales of *A. seddoni* attributed to the five separate scale morphology regions on the thelodont body

undescribed, thelodont remains have been found in the Lawford Ranges (Turner and Young, 1992; Turner, 1997). Some of these scales have been compared to *Turinia antarctica* Turner and Young, 1992 but Turner (1994, 1997) referred others to *A. seddoni*. With the discovery of greater variation in the scales of *A. seddoni* it is probable that these scales can be now verified as belonging to *A. seddoni*. Outside Australia *Australolepis* was tentatively reported from the Holy Cross Mountains fauna in Poland (Ginter, in Turner, 1995). However, it is now thought that these scales may in fact be

chondrichthyan (Turner, 1997). Scales of *A. seddoni* occur in the early Frasnian deposits at Kale-Sader in the basal Shishtu Formation in eastern Iran (Turner, 1997; Yazdi *et al.*, 1998). The discovery of a second thelodont in the Gneudna Formation also supports the closeness of the Frasnian faunas from eastern and central Iran to those in Western Australia.

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